BLEEDING AND COAGULATION IN SOME BERMUDAN CRUSTACEA [1]

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The blood of crustaceans has long been of interest to zoologists and many observations on the coagulation function are to be found in the early literature. Glavand (1948) cites a score of studies prior to 1893, two dozen more between this date and 1920 but only a handful thereafter. These studies consider the nature of crustacean coagulation, contrasting it to that in vertebrates, and a number compare various species in regard to intensity and type of mechanism. Tait (1911) recognized three types of animals: first, those with cellular agglutination alone; second, those with cellular agglutination together with some further clotting of the plasma (*i.e.*, with fibrinogen); and third, those with negligible cellular agglutination but substantial clotting of the plasma. The second group, those with both mechanisms, forms a continuous series of intergrades between the first and third groups with either agglutinating cells or fibrinogen. These distinctions were all based on qualitative observations as to the strength and properties of the coagula since no quantitative measurements of the mass of cellular material or of fibrinogen were made. Even Glavand's recent careful study on the lobster (1948) gave only a rough average value for the normal fibrinogen level in this species. Such information is of interest in evaluating the coagulation function in various invertebrates and in comparing it to that in vertebrates.

Materials and Methods

Animals

Some 150 individuals representing 12 species were collected by hand or trapped in an 8-week period in the summer of 1946. The availability of these various crustaceans is indicated in Table I where the numbers, weight range, sex, habitat and mode of capture of these animals are summarized. All specimens were caught personally except for the spiny lobsters which were taken by commercial fishermen and the locust lobsters which came from the Bermuda Aquarium through the kindness of its director, Mr. Louis Mowbray.

A number of other species were collected but not studied because only one or two specimens were available and/or because the species were too small to allow effective collection of blood. These included the ghost crab (*Ocypode arenarius*), the gulfweed crab (*Planes gracilis*), the flat crab (*Percnon planissimum*), the spider crabs (*Mithrax forceps, Microphrys bicornutus* and *Macrocoeloma trispinosum*), petrolisthes (*Petrolisthes armatus*), the red-hermit crab (*Calcinus sulcatus*),

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TABLE I

General characteristics of the species studied

Species	Weight in gm.	No. ♂	No. ♀	With eggs	Location	Capture
Portunidae						
Callinectes ornatus	50–85	9			Sheltered muddy bay, free swimming or buried	Net or trap
C. danae (Bermuda blue crab)	50–140	3	2			
C. sapidus (common blue crab)	165–380	4				
Achelous smithii	100–115				Sheltered channel or open bay	Trap
Piluminidae						
Eupanopeus herbstii	10–59	17	11	3	Sheltered bay; in or on muddy bottom	Trap or under stones
Grapsidae						
Plagusia depressa (cliff crab)	34–130	10	11	4	Rocky open shore, always in water	Net
Grapsus grapsus (rock crab)	25–105	11	14	6	Rocky open shore, in or out of water	Hand or net
Goniopsis cruentatus (Mangrove crab)	18–43	9	8	2	Mangrove swamp, in or out of water	Trap
Gecarcinidae						
Gecarcinus lateralis (common land crab)	1.8–27	19	18	4	Stony island or beach	Under stones
Paguridae						
*Dardannus venosus** (red-veined hermit crab)	56				Sheltered channel	Trap
Palinuridae						
Panulirus argus (spiny lobster)	150–4500				Reef	Trap
Scyllaridae						
Scyllarides aequinoctialis (locust lobster)	720–870				Reef	Trap

* The only large hermit crab listed for this region. In this specimen, however, the right chela was the larger.

the tri-colored hermit crab (*Clibanarius tricolor*), *Glypturus branneri* and the "split thumbs" (*Gonodactylus oerstedii* and *Pseudosquilla ciliata*). (Nomenclature follows Verrill, 1908, 1922.)

The rock crab (*Grapsus grapsus*) was perhaps the most abundant large crustacean on the island but because of its agility and thin shell it was very difficult to capture uninjured specimens by ordinary means. At night, however, these animals could be approached with a light and picked up directly from the rocks where they lay just above the waterline. By this means 5 were taken in 15 minutes on one occasion and 7 in 25 minutes on another, as compared to 5 animals taken alive in

two hours by two men during the day. These crabs killed one another in a small container or tank and seemed to survive poorly when this was prevented by removing the chelae. In a large tank with a screened enclosure which permitted them to come out of water, they remained healthy and vigorous for several weeks. Another large grapsoid crab with a heavier shell, the "cliff" crab (*Plagusia depressa*), was taken in considerable numbers although it is listed as "rare" by Verrill (1908). Belying its name, it was never seen above water but as many as 10 to 14 were taken from just below the water line along rocky shores on still sunny mornings.

Bleeding

The animals were bled from the limbs after amputation, usually within 4 to 20 hours of capture. Usually the chelae were cut first and then one of the larger walking legs. The courses of two representative bleedings are shown in Figure 1. Although coagulation occurred quickly in the collecting vial, usually within a minute, it was often many minutes before flow stopped at the limb. Bleeding was encouraged by holding the cut stump downward and by maintaining pressure on the carapace. After the flow had stopped at one limb or following autotomy, another was amputated, usually with a renewed flow, but this procedure was seldom effective beyond the second or third limb (Fig. 1). There was characteristically a quite abrupt end-point beyond which no more blood could be obtained from the animal despite the application of pressure, time or further amputation.

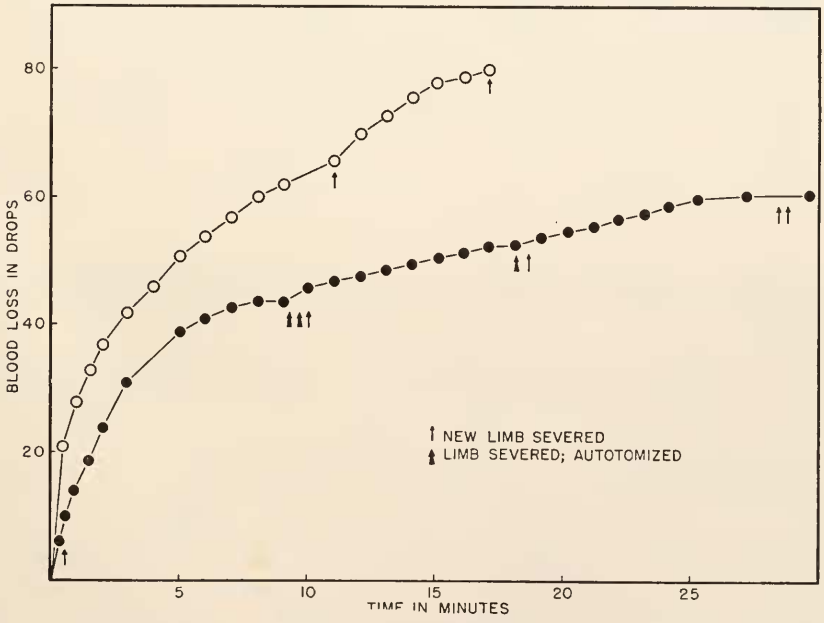

FIGURE 1. Course of bleeding in two representative individuals. Open circles, *Callinectes danae*, 76 g. ♂; bleeding volume 7.0 cc.; average drop, 0.09 cc. Closed circles, *Gecarcinus lateralis*, 27 g. ♂; bleeding volume 3.6 cc.; average drop, 0.06 cc. After an initial rush of blood the bleeding volume was roughly proportional to the square root of the elapsed time ($V = kt^{\frac{1}{2}}$).

Coagulation

The term coagulum will be used to describe the total product of the two processes, the agglutination of cells and the polymerization of fibrinogen into fibrin. In some species this coagulum is largely a cellular agglutinate while in others it is largely a fibrin clot.

TABLE II

The bleeding volume in various Crustacea

Genus	No.	Ave. wt. g.	Bleeding volume in cc./100 g.		
			Range	Mean	σ
Gecarcinus	35	12	5.6–13.9	9.5	2.8
Grapsus	31	72	4.0–10.8	6.6	1.9
Goniopsis	13	25	4.1–10.5	6.9	2.1
Plagusia	28	75	3.3– 8.8	5.5	1.6
(Grapsidae)	72	64		6.2	(27%)
Eupanopeus	25	29	1.3– 7.1	3.8	1.5
Callinectes	13	130	6.9–18.8	10.5	3.2
Achelous	2	108	6.0– 7.0	6.5	—
(Portunidae)	15	127		10.0	(36%)
(*Brachyura*)	147	53		6.9	
Dardannus	1	56		5.0	—
Panulirus	3*	270	(4.0–10.7)	(6.7)	
	1	4,500		20.0	
Scyllarides	2	800	15.3–18.5	16.9	
Cambarus	7	34	6.0–10.9	8.6	2.0

* Bleeding discontinued before maximum volume obtained.

As the blood dropped from the cut limb it was kept agitated so that the coagulum continuously synerized out as it was formed. In strongly clotting, fibrinogen-containing bloods (*e.g., Panulirus* and *Callinectes*) this was difficult and it was necessary to break up the clot and press out the serum through gauze. Following syneresis the coagulum was washed for half-hour periods successively in 1% sodium chloride and in water to remove soluble organic constituents, largely hemocyanin, and inorganic salts (Morrison, 1947). This step was doubly important in some of these animals because of the high blood salt content and the often imperfect syneresis which resulted in a residue with a considerably higher water content than is obtained from mammalian clots. However, some soluble cellular components were also undoubtedly removed by this extraction process. The synerized and extracted coagulum was then dried at 105° C. for 48 hours and stored in vials between layers of lens paper, since a balance was not available. Later, after a subsequent 48-hour drying period the coagulum was weighed to 0.1 mg. In smaller species the blood from several individuals was pooled in order to obtain a sufficient quantity of coagulum.

Results and Discussion

Bleeding volume

The data on bleeding volumes in the several species are summarized in Table II. Individual values within a species varied over a three-fold range and average values ranged from 3.8 in *Eupanopeus* to 16.9 cc./100 grams of body weight in *Scyllarides*. The values for the Macrurans averaged higher (13 per cent) than the Brachyurans (7 per cent) and of the latter the swimming Portunids averaged somewhat higher (10 per cent) than the others (6.5 per cent). Part of this latter difference undoubtedly derives from the fact that the climbing or crawling crabs bear a considerably heavier weight of shell than do the lighter swimming or walking species. Thus, values for the per cent of body water ranged from 53 and 54 in *Plagusia* and *Eupanopeus* to 76 and 78 in *Callinectes* and *Gecarcinus*. Bleeding volumes expressed as per cent of the body water were, with the exception of *Eupanopeus* (7.0), much more constant, ranging from 10.4 in *Plagusia* to 13.8 in *Callinectes*.

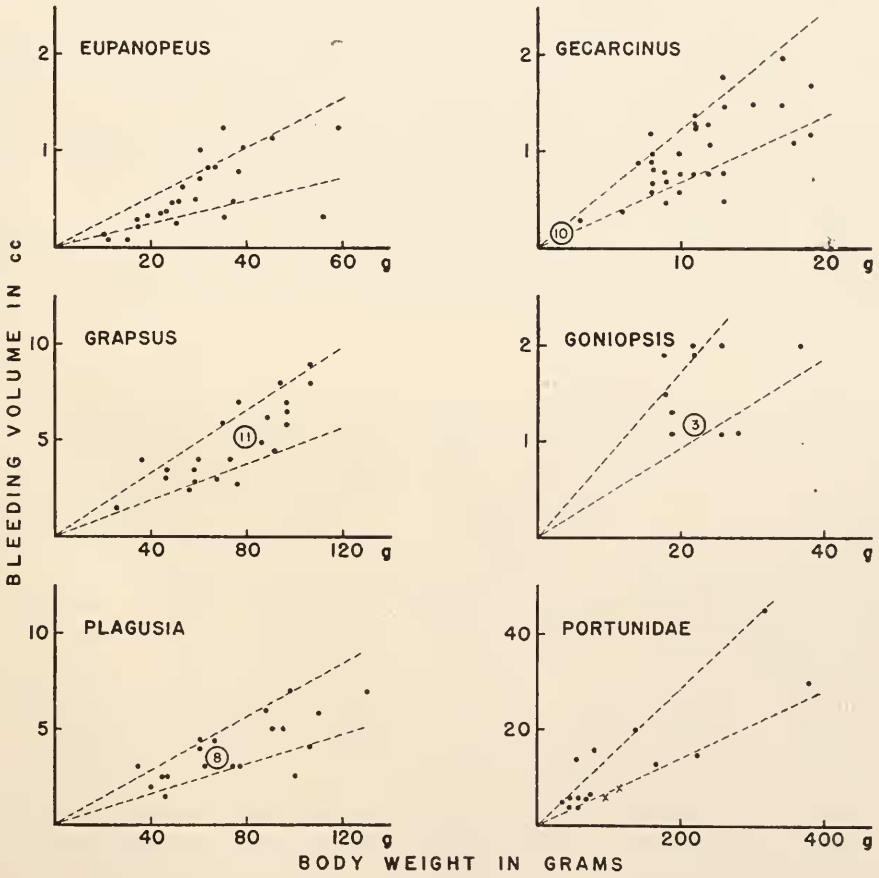

Figure 2. Bleeding volume in 6 genera of Crustacea as a function of body weight. Symbols show individual values except the circles which represent pools of the indicated size. Broken lines show standard deviations.

Bleeding volumes for 6 of the species are plotted as a function of body weight in Figure 2. Some tendency toward lower per cent yields in the smaller individuals is seen in *Grapsus* and particularly in *Eupanopeus,* and this may in part account for low bleeding volume in the latter species. A similar group correlation with weight may be seen since the heavier Macrurans have the largest bleeding fraction, the Portunids are next and the smaller Brachyurans are last. This correlation breaks down in comparing the three smallest genera, however, since of these the lightest, *Gecarcinus* (12 g.), has the largest bleeding fraction followed by *Goniopsis* (25 g.) and *Eupanopeus* (29 g.).

These crustacean bleeding fractions of 4 to 17 compare to a total blood volume of 25 cc./100 g. as measured in crayfish (*Cambarus virilis*) by Prosser and Weinstein (1950), using dye dilution methods with T-1824 or thiocyanate. Measurements of the bleeding volume on this same species gave values ranging from 6 to 11 and averaged 8.6 cc./100 g. (Table II). Since this value is only one-third of that obtained by dye dilution, it is evident that much blood is left behind in bleeding. On the other hand, the bleeding volume results from a fairly discrete end point and is reasonably constant. Indeed, the standard deviation of bleeding volumes averaged less than 30 per cent of the mean (20 per cent in *Cambarus*) as compared to 36–38 per cent for the blood volume in the dye dilution study referred to above. It seems possible, therefore, that the bleeding volume may represent some definite fraction of the total blood volume, perhaps that fraction occupying the heart, blood vessels and large sinuses since this would be the most readily expressed. With this concept in mind it is of interest that the bleeding volume bears the same relation to the blood volume (T-1824 or NaCNS) in the crayfish (1:3) with its open circulation as the blood volume (T-1824) bears to the extracellular volume (NaCNS) in the frog (1:3.3) or mammal (1:3–4) with their closed circulation (Prosser and Weinstein, 1950).

Coagulation; general description

The initial step in coagulation, which removed the cellular elements, usually began and was completed within a minute. Before this time the freshly drawn blood was opaque but thereafter it was clear although often strongly colored by hemocyanin and/or other blood pigments. In *Eupanopeus, Gecarcinus* and the Grapsidae this initial coagulum was fairly substantial and little if any further clotting could be distinguished. In *Panulirus,* however, the initial stage was often represented by only a few shreds of material and the first intimation of clotting was a sudden gelation of the solution. If the clotting solution is undisturbed the gel is very transparent, rigid, elastic and synerized only with difficulty. These are all properties which characterize a "fine" clot containing small structural fibers (*ca.* 100 Å) and interstices such as is formed from mammalian fibrinogen under conditions of high pH and fibrinogen concentration (Ferry and Morrison, 1947).

Under physiological conditions mammalian fibrinogen forms a coarser structure than crustacean fibrinogen, a distinction which was first observed by Howell (1916) under the ultramicroscope. Stubel (1920) also described the transformation of invertebrate fibrinogen as into small "granules" rather than into the long "needles" characteristic of mammalian material. In the amphibians and fishes, however, fine structured clots are seen in both gross and microscopic observation (Stubel,

1914). Among the vertebrates this difference in clot structure may be correlated with differences in the solubilities of the respective fibrinogens (Morrison, Scudder and Blatt, 1951). The more soluble fibrinogens found in the lower vertebrates may represent smaller, less asymmetric and/or more highly charged molecules, any or all of which conditions could account for the "finer" clots formed from them. That a similar situation may exist in crustacean fibrinogen is further suggested by the observation of Glavand (1948) that a relatively high gel fraction (*ca.* 1.5 g./1.) was necessary for clotting in these animals. A gel fraction of as little as 0.05 g./1. is sufficient to form a continuous clot in systems with mammalian fibrinogen (Ferry and Morrison, 1947).

Coagulum weights

Average weights for the coagula are summarized in Table III. Values by species ranged from 3.6 g./1. in *Plagusia* to 16.6 g./1. in *Panulirus*. Individual values are very variable, with standard deviations averaging about 50 per cent and with as much as an eight-fold difference being observed in *Callinectes*. Such variation in the coagulating ability of crustacean blood has been noted before. Cuénot (1891) reported that strength of the clot varied much more than the level of hemocyanin in blood from starving crabs and lobsters. Similarly, Glavand (1948) found that the fibrinogen in lobster blood often disappeared entirely during captivity. In this study the two locust lobsters had been held in captivity in the Bermuda Aquarium for a number of months which may account for the smaller coagulum, negligible in one specimen, and the longer clotting time as compared to the spiny lobsters which were freshly trapped. Similar changes in nutritional or other conditions in the natural trapped specimens may be responsible for the high variability observed here. The natural variability of fibrinogen in the lady crab, *Ovalipes*, was apparently so great that Loeb (1903) first reported it to be absent in this species and then subsequently (1904) reported it to be present.

Gruzewska (1932) related lower fibrinogen levels in the green crabs (*Carcinides maenas*) to moulting. Values for the only two soft-shelled (blue) crabs taken in this study were not included in the average values in Table III. These values (2.4 and 2.5 g./1.) are among the lowest found in this group being less than half of the mean value.

The Macrurans formed much heavier coagula (average = 17 g./1.) than the Brachyurans (average = 5 g./1.). This agrees with the qualitative observations of much more effective clotting in European Macrurans as reported by Cuénot (1891) (*Palinurus*), Heim (1892) (*Palinurus, Homarus*), Tait (1911) (*Palinurus, Homarus* and *Astacus*), and Glavand (1948) (*Homarus* and *Nephrops*), and in *Homarus americanus* by Loeb (1904).

Large differences in clotting ability are found among the various Brachyurans. Heim (1892) and Tait (1911) both mention *Portunus puber* as the one species among many crabs which approaches the Macrurans in this regard and Loeb (1904) and George and Nichols (1948) refer to the firm clots in the related *Callinectes*. In Table III it may be seen that the Portunidae do average somewhat higher (5.8 g./1.) than the Grapsidae (4.0 g./1.) but because of the high variability the difference is barely significant ($t = 2.7$). Of more interest, and correlating with the very firm clots often observed in this group, may be the fact that the highest indi-

TABLE III

Coagulum weights in various Crustacea

Genus	No.*	Coagulum in g./l.			Clotting time** sec.
		Range	Mean		
*Gecarcinus***	10	2.1– 5.6	3.6	1.2	44
Grapsus	17	2.6– 6.2	4.1	1.2	
Goniopsis	5	2.5– 6.3	4.0	2.1	
Plagusia	3	3.0– 4.3	3.6	0.9	35–120
(Grapsidae)	25		4.0	(33%)	
Eupanopeus	7	3.0– 7.2	4.7	1.8	5–90
C. ornatus	8	1.5–13.0	5.0	4.7	60
C. sapidus	3	5.0– 7.4	6.2	1.5	60
C. danae	3	2.5– 9.8	8.6	1.6	60
Achelous	2	2.1– 5.5	3.8	2.8	52–75
(Portunidae)	16		5.8	(43%)	
(*Brachyura*)	63		4.8		
Dardannus	1		15.6		
Panulirus	7	8.6–22.3	16.6	5.0	
Scyllarides	2	(1.8– 8.9)	(5.3)		300
*Cambarus****	5	1.1– 3.3	2.1	1.0	40–65

* Each value represents a pool of 1 to 6 individuals.

** Blood delivered from limb into a glass vial; time measured to the first appearance of a clot; values represent 1 to 3 observations.

*** Excluding value of 1.5 g./l. for a pool from 10 very young (average weight = 1.8 g.) individuals.

**** Commercially supplied individuals from Wisconsin. Time after capture not known.

vidual values (to 13.0) were found in the Portunidae. Only one Anomuran species was studied. The single *Dardannus,* a large hermit crab, had a higher value (15.6 g./l.) than any of the Brachyurans. This may correlate with the lesser defense against injury provided by its soft body.

Agglutination vs. clotting

In this study measurements of fibrinogen alone were not made but only of the extracted coagulum which also contained cellular components. One might estimate the fibrinogen level in those animals possessing it by subtracting from the weight of the coagulum, an amount equal to that in those species which are considered not to have fibrinogen. But a simple correction of this sort is of questionable validity since it assumes that the various species have comparable amounts of cellular material. This is certainly not the case since Yeager and Tauber (1935) found cell counts ranging from 5×10^3/mm.^{3} in *Talorchestia* to 54×10^3/mm.^{3} in *Callinectes* (average $= 18 \times 10^3$/mm.^{3} in 13 species of crustaceans) with an individual standard

deviation of 30 to 60 per cent. Similarly, George and Nichols (1948) found a hematocrit value of 1.0 per cent in *Callinectes* but only 0.25 per cent in *Libinia*. The species with distinct fibrinogen clotting also appear to have more cells. Although these additional cells do not necessarily represent agglutinating components they will nonetheless become enmeshed in the clot structure and contribute to the weight of the coagulum. Still, even in *Callinectes,* the form most abundantly supplied with cells, the dry cell weight presumably amounts to only 20–25 per cent of the cell volume or 2–2.5 g./l. and the extracted dry weight should be even less. In *Libinia* and other species with fewer cells, a value of only 1/2 to 1/4 the above or 0.5–1.2 g./l. is expected. Since average values of about 4 g./l. (3.6–4.6 g./l.) or 3 to 8 times the above estimate were found even in the five lowest species in Table III, it would appear that considerable material had been adduced to the cellular components from the plasma even in those species which show only an "initial" coagulation phase and which formerly had been considered to have no fibrinogen in their plasma. However, although this unidentified material precipitates from plasma on the shedding of blood it should perhaps indeed not be considered as fibrinogen since it does not form the gel structure which we are accustomed to associate with fibrin.

Using a correction of 1–2 g./l., the dry cell weight estimated above, we arrive at a mean value of 3 g./l. for the plasma component in *Eupanopeus, Gecarcinus* and the Grapsidae. In the spiny lobster, *Panulirus,* the fibrinogen value is five times this amount or 15 g./l. and individual values range up to 20 g./l. Glavand (1948) reported values for the fibrinogen level in the common lobster, *Homarus vulgarus,* ranging from 2.9 to 10.9 g./l. and stated (p. 96) that "fibrinogen of about 0.4 per cent (4 g./l.) in the citrated plasma is as a rule found." These values are considerably lower than those in the spiny lobster but the Palinuridae, *i.e., Palinurus,* have been previously cited as having the most strongly clotting blood of any of the crustacea, including the other Macrurans (Tait, 1911).

Mammalian vs. crustacean fibrinogen levels

It is of considerable interest to compare the fibrinogen level in mammals to that in these crustaceans. The clot formed by the blood of *Panulirus* is certainly equal and probably superior to an ordinary mammalian clot in strength and rigidity. However, this appears to be achieved only by the use of a considerably larger amount of material (15 g./l.) since the normal fibrinogen level in mammals is at only 2–4 g./l., although in some species, *e.g.,* swine and cattle, values up to 8–10 g./l. have been reported. In the less effective of the crustaceans the coagulum weight was roughly equal to the fibrinogen level in many mammals, but in functional terms of gel formation the two groups cannot even be compared.

In terms of variability a striking contrast is seen between the mammals and the crustaceans. Gram (1921) in measurements on 50 men and women found an average value of 2.8 g./l. with a *range* of ± 30 per cent. Similarly, Ham and Curtis (1938) found an average value of 2.5 g./l. with a *range* of ± 28 per cent in 38 normal men and women. These values of ± 30 per cent for the *range* of variation in sizable groups of men compare with *standard deviations* of about 40 per cent in the Crustacea. The latter value is low since a number of the individual values upon which it was based represented pools of blood from up to six individuals. The difference is even more striking in single individuals which in

the crustaceans can lose all coagulation function (Glavand, 1948) but which in man vary by only ± 4–8 per cent from the mean over periods of more than a year (Gram, 1921; Ham and Curtis, 1938). It should be noted, however, that fibrinogen levels of up to 7 g./l. have been recorded in man in response to a variety of infectious diseases (Ham and Curtis, 1938).

Coagulation and hemostasis

Some inverse correlation between autotomy and clotting ability may be seen in the fact that the heaviest clots came from a genus (*Panulirus*) in which it is difficult to induce the autotomy of even a single limb while the lightest clots came from genera (*Gecarcinus, Eupanopeus* and the Grapsidae) which are very prone to autotomy. Tait (1911) considered this proposition, *i.e.,* that these two hemostatic mechanisms might substitute for one another, and although most of his data

TABLE IV

*Hemostatic influences in various arthropods**

Genus	Size	Shell	Autotomy	Cells	Fibrin	Σ+	Reference**
Limulus	+	++	0	++++	0	7	d
Libinia	++	++++	+	+	0	8	d,g
Maia	(++)	+	+++	+	0	7	b,g
Gecarcinus	+++	+	++++	+	0	9	a,g
Goniopsis	+++	++	+++	+	(0)	9	a
Plagusia	++	++++	++	+	(0)	9	a
Grapsus	++	+++	++	+	(+)	9	a
Eupanopeus	+++	++	++	++	0	9	a,g
Cancer	++	+++	+	+	+	8	e,f,g
Carcinides	++	++	++	+	+	8	e,f,g
Callinectes	++	++	++	+	++	9	a,d,g
Portunus	++	++	++	+	+++	10	c,e,g
Dardanus	+++	+	(+)	?	+++	8	a
Astacus	+++	++	+	0	+	7	e,c,f,g
Cambarus	+++	++	+		+	7	a,g
Homarus	+	+++	+	+	++	8	d,f,g
Scyllarides	+	++	++		++	7	a
Panulirus	+	+++	+	(0)	+++	7	a
Palinurus	+	(++)	++	0	+++	8	b,c,e,g
Isopods	+++	+	0	?	+++	(7)	e

* Average adult size as *small* (< 60 g.), +++; *medium* (60–300 g.), ++; or *large* (> 300 g.), +. Shell weight as *light* or *absent*, +; *moderate*, ++; *heavy*, +++; or *very heavy*, ++++. Tendency toward autotomy as *very strong*, ++++; *strong*, +++; *moderate*, ++; *weak*, +; or *absent*, 0. "Cellular agglutinate" (initial coagulum) or fibrin clot as *heavy*, +++; *moderate*, ++; *light*, +; or *negligible*, 0.

** References: a, this study; b, Cuénot (1891); c, Heim (1892); d, Loeb (1903); e, Tait (1911); f, Glavand (1948); g, Wood and Wood (1932).

were affirmative he felt that two notable exceptions invalidated the principles. Possibly he attempted too great a simplification since fibrinogen and autotomy are not the only factors which affect the potential loss of blood in crustaceans. The agglutinating cellular constituents certainly facilitate hemostasis and the strength of the shell must be important in preventing injuries which might cause blood loss. The over-all size of the individual may also be important since a given thickness of shell will afford less protection to a large animal than a small one. Further, bleeding from a large limb would be more diffcult to staunch than from a small limb. Indeed, in the smaller Crustacea it was often not possible to obtain even a drop of blood from the severed appendage.

The interrelations of these several factors in a number of arthropods are summarized in Table IV where arbitrary grades of intensity have been assigned to the several quantities. The sums of these various values are tabulated in column 6 and show reasonable constancy for the various species. Thus, while the spider crab, *Libinia,* has neither fibrinogen nor effective power of autotomy it is very strongly protected by its shell. *Gecarcinus,* on the other hand, which has protection from neither shell nor fibrinogen has a highly developed power of autotomy. Again, the spiny lobster with little capacity for autotomy and not too heavy a shell in relation to its large size possesses a high concentration of fibrinogen while *Limulus,* with similar disadvantages, compensates by a copious cellular agglutination. Other crabs, *Callinectes, Carcinides* and *Grapsus,* in contrast, appear to utilize all of the mechanisms but each in moderate extent. In brief, then, hemostasis appears to be an important function in these animals, but one which may be accomplished either singly or in concert by a variety of very different means.

Summary

1. Maximum bleeding volumes and coagulum weights were determined on more than 150 individuals of 12 species of Bermudan crustaceans.

2. Average values for the bleeding volume ranged from 3.8 cc./100 g. in *Eupanopeus* to 16.9 cc./100 g. in *Scyllarides* and averaged 7.2 cc./100 g., an amount equal to roughly one-third of the true blood volume in crustaceans but about equal to the blood volume in vertebrates.

3. Average values for the weight of the extracted and dried coagulum representing the sum of fibrin and cellular constituents ranged from 3.6 g./l. in *Plagusia* to 18.1 g./l. in *Panulirus* with large individual variation in most species.

4. Even in animals previously considered to possess only an "initial," cellular phase of coagulation, the coagulum weights were 3–8 times greater than the estimate of the maximum cellular contribution and it was concluded that plasma components must be of importance in these species.

5. In species possessing considerable amounts of fibrinogen a "fine-structured" clot is formed resembling that in lower vertebrates rather than that in mammals. The mechanical properties of this clot compare favorably to the mammalian clot but 3–6 times as much fibrinogen is employed.

6. A comparison of species with regard to the various factors modifying hemostasis, *i.e.,* fibrinogen, agglutinating cells, autotomy, size, and shell strength shows a compensation whereby animals lacking one or more mechanisms were particularly strong in others.

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